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Effects of Seasonality on Brain Size Evolution: Evidence from Strepsirrhine Primates

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ABSTRACT: Seasonal changes in energy supply impose energetic constraints that affect many physiological and behavioral characteristics of organisms. As brains are costly, we predict brain size to be relatively small in species that experience a higher degree of seasonality (expensive brain framework). Alternatively, it has been argued that larger brains give animals the behavioral flexibility to buffer the effects of habitat seasonality (cognitive buffer hypothesis). Here, we test these two hypotheses in a comparative study on strepsirrhine primates (African lorises and Malagasy lemurs) that experience widely varying degrees of seasonality. We found that experienced seasonality is negatively correlated with relative brain size in both groups, controlling for the effect of phylogenetic relationships and possible confounding variables such as the extent of folivory. However, relatively larger-brained lemur species tend to experience less variation in their dietary intake than indicated by the seasonality of their habitat. In conclusion, we found clear support for the hypothesis that seasonality restricts brain size in strepsirrhines as predicted by the expensive brain framework and weak support for the cognitive buffer hypothesis in lemurs.

Keywords: energetic constraints, periodic food shortage, phylogenetic comparative method, Lemuriformes, Lorisiformes.

Introduction

Many physiological and behavioral adaptations of animals reflect characteristics of their habitats. Indeed, it is known that the variability of environmental conditions over time, or degree of seasonality of a habitat, influences traits such as body size, group size, group composition, and home range size (e.g., Eeley and Foley 1999; Nunn 1999; Strier et al. 1999; Ostner et al. 2002; Lehman et al. 2005; Plavcan et al. 2005). However, there is neither much theory nor empirical information about the relationship between habitat seasonality and brain size. In this article, we develop and test detailed predictions that arise from two hypotheses: the expensive brain framework and the cognitive buffer hypothesis.

First, considering that brain tissue requires a high and uninterrupted supply of energy (Mink et al. 1981) and building on earlier hypotheses about energetic constraints on brain size evolution (e.g., Aiello and Wheeler 1995), the expensive brain framework (Isler and van Schaik 2009) proposes that an increase in brain size relative to body size is possible only if total energy metabolism is increased or the energy allocation to other functions is reduced or both. Since serious starvation leads to permanent brain damage (Lukas and Campbell 2000), we expect brain size to be constrained if in a seasonal habitat the energy supply is periodically low, even if physiological buffers such as fat storage, reduced activity, or hibernation allow survival. Frequently, animals change to fallback foods that are of lower dietary quality than the preferred diet but are more abundant or not seasonally scarce (Hemingway and Bynum 2005). Such diet shifts also represent a physiological buffer, since the total net energy available per day is still reduced during the lean period; that is, the animal still experiences the seasonality of its habitat. Each species is adapted to its preferred or staple diet morphologically. If it would be able to fully compensate (or even overcompensate) for the change in diet during lean periods, for example, by increasing foraging effort, and thus be better adapted to fallback foods, these foods would become its staple diet also during the good periods (as is the case in many folivorous primates). Of course, some differences in brain size may result from the main adaptation, and therefore, it is important to control for diet type when testing the correlations between seasonality and brain size.

All physiological buffers entail a seasonally reduced energy budget, but the costs of brain function are not reduced (except probably in deeply hibernating rodents; Krilowicz et al. 1988). The central prediction of the expensive brain framework is therefore that, all other things being equal, the average brain size within a population is negatively related to the duration (and perhaps frequency) of periods

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of low food availability that cannot be fully compensated for by increased foraging effort. To test this prediction, we use the temporal variation in the consumption of the diet component with the highest nutritional value (i.e., preferred food item) as an index for the degree of variation in energy intake, henceforth referred to as "experienced seasonality." To enhance comparability with other studies and to explore possibilities for future studies, we also investigate how well experienced seasonality is predicted by climatic variables—annual variation in rainfall and temperature (Janson and Chapman 1999)—and a more direct measure of plant productivity, the normalized difference vegetation index (NDVI; Pettorelli et al. 2005).

This prediction from the expensive brain framework enjoys some empirical support from a similar phenomenon, island dwarfism. Many mammals show dwarfing on small islands where high population densities may produce resource shortages (Filin and Ziv 2004; Lomolino 2005), especially in relatively large-bodied species (the opposite phenomenon, island gigantism, is found in relatively small species if predation pressure on an island is reduced but food resources are not limited). Köhler and Moyà-Solà (2004) suggested that dwarf island forms of a rupicaprine bovid (*Myotragus*) are relatively smaller brained, and they linked the relative reduction in brain size to limited resources. Based on this, Niven (2007) discusses potential impacts of resource limitations on brain size in the hominin *Homo floresiensis*. Weston and Lister (2009) have made the same argument for *Hippopotamus* species on islands. Similarly, Taylor and van Schaik (2007) argued that a subspecies of Bornean orangutans living in a region with more frequent El Niño–induced droughts and forest fires is relatively smaller brained because it is forced to feed largely on the nutritiously poor inner bark of trees more than are other orangutans.

The second hypothesis predicts the opposite pattern. The cognitive buffer hypothesis (Allmann et al. 1993) assumes that relatively large-brained species benefit from enhanced cognitive abilities. Seasonal habitats are likely to be more cognitively demanding than nonseasonal habitats because preferred food sources are more dispersed in space and over time. Larger-brained individuals would therefore perform better in seasonal habitats because their enhanced cognitive abilities will facilitate flexible behavioral responses to the fluctuating environment. Thus, we would expect selection to favor relatively large brains in seasonal habitats. This hypothesis is supported by a comparative study on Neotropical parrots, which found a positive correlation between climatic variability and brain size (Schuck-Paim et al. 2008). Moreover, migrating birds have smaller brains than nonmigrating species (Winkler et al. 2004; Sol et al. 2005), which the authors interpret as a cognitive buffer effect in the residential species.

The two effects may also operate in combination. If the energetic constraints predicted by the expensive brain framework holds, the presence of a cognitive buffer effect would reduce the negative correlation between brain size and seasonality in energy availability. Thus, to test whether both cognitive buffer effects and energetic constraints operate, we look for a dampening of the environmental seasonality through increased energy intake. The combined expensive brain–cognitive buffer hypothesis predicts that in relatively large-brained species, the seasonality experienced by the animals (i.e., temporal variation in energy intake) is far less than the seasonality of the environment they live in (fig. 1).

In this study we test these predictions in two groups of strepsirrhine primates, the African lorises and the Malagasy lemurs. Both groups are of small to medium body size and more encephalized than the average mammal, and they thus devote a relatively large percentage of basal metabolism to brain maintenance (11%–12% as compared

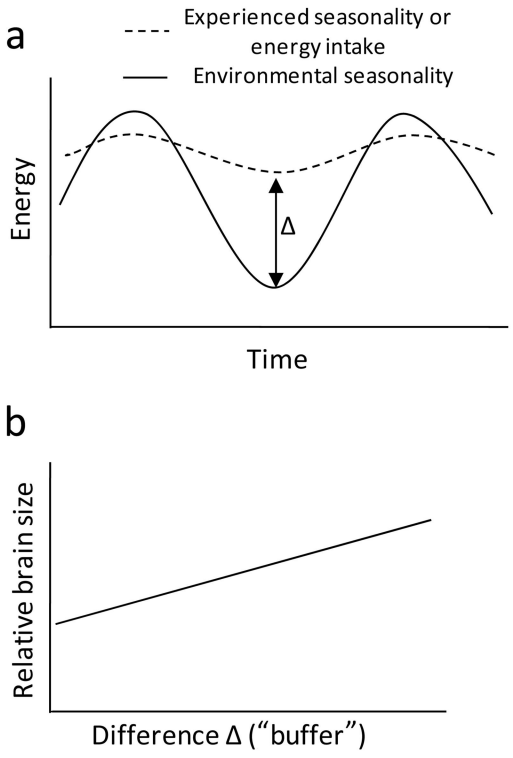

Figure 1: *a*, A large difference Δ between experienced and environmental seasonality would imply a large dampening effect ("*buffer*") through behavioral flexibility. *b*, Even if energetic constraints result in an overall negative correlation between relative brain size and experienced seasonality, cognitive buffer effects would result in a positive correlation between relative brain size and the difference between environmental and experienced seasonality.

with 8%–9% in cercopithecoid primates, as calculated from Mink et al. 1981; Isler et al. 2008). Godfrey et al. (2001) and Catlett et al. (2010) showed that age at weaning is positively (or dental precocity is negatively) correlated to brain size in lemurs, but otherwise strepsirrhines do not exhibit the usual correlates of encephalization found in anthropoid primates, such as group size (Shultz and Dunbar 2007; MacLean et al. 2009) or diet quality (Fish and Lockwood 2003).

The lemurs are particularly interesting, as they are endemic to Madagascar, a large island with strong and varied climatic seasonality (Dewar and Richard 2007). The eastern part is characterized by high annual rainfall, and a low degree of within-year climatic seasonality is struck in some years by extreme climatic conditions (storms and cyclones; see Ganzhorn 1995). The much-larger western part is extremely seasonal within a year for such latitudes but more predictable between years. In response, lemurs have evolved a great variety of special adaptations to cope with the seasonality of their environment (Ganzhorn et al. 1999; Wright 1999): almost all species show extreme birth seasonality (Janson and Verdolin 2005), the basal metabolic rates of most species are below those of haplorrhine primates (Genoud 2002), and the only two species of primates that show torpor or hibernation are lemurs (Dausmann et al. 2004; Schülke and Ostner 2007). As lemurs are thus a highly diverse group of primates, it is necessary to test whether environmental seasonality is a good proxy for energy intake or whether we must use more direct measure of experienced seasonality. If environmental seasonality and experienced seasonality differ, we can use the difference between the two to test whether relatively large-brained lemur species cognitively buffer the impact of their seasonal environment.

For African lorises, detailed data on monthly diet composition throughout the year are largely unavailable (Charles-Dominique 1974; Harcourt 1986); thus, an analogous test is not possible. However, since all African lorises are nocturnal and arboreal and their diets are homogeneous and largely insectivorous (Rowe 1996), we assume that environmental seasonality directly reflects seasonality of energy intake in this group. Insect availability follows rainfall seasonality more than it does the production of new leaves (Wolda 1978; Coley and Barone 1996). Leaf production can differ considerably from rainfall if, as in central Africa, plant productivity is not limited by rainfall but by irradiance (Wright and van Schaik 1994). We therefore assume that variation in rainfall and temperature, as a proxy for irradiance, are more reliable proxies for experienced seasonality than plant productivity in the African lorises.

Methods

Brain and Body Size

Endocranial volumes from 428 skulls were measured using glass beads in eight European and four American museums, and these data were added to the data set of Isler et al. (2008) for a total of 1,049 skulls (from 507 known locations). Only adult specimens (third molar present) for whom the original provenance was known were included in our sample, in order to exclude a possible effect of captivity. In total, our sample comprises 934 adult individuals from 36 lemur species from 215 locations and 15 loris species from 241 locations (table A4 in the online edition of the *Amercian Naturalist*).

It has been documented that primates tend to have smaller body sizes in more seasonal habitats (Albrecht et al. 1990; Lehman et al. 2005; Plavcan et al. 2005). It is therefore important to include body size as a covariate in the analyses. Body masses from wild study populations were collected from literature sources (table A4). In their monumental compilation of primate body masses, Smith and Jungers (1997) also included body weights from populations of the Duke Lemur Center in Durham, North Carolina, but since there is a large captivity effect on body mass (Isler et al. 2008), we did not include studies on body weights from the Duke Lemur Center. Male and female body mass and endocranial volumes were pooled, since most strepsirrhine primates do not exhibit sexual dimorphism in body mass (if it exists, females tend to be slightly heavier; see Kappeler 1997).

For seven out of 36 species, no wild body mass data were available. Therefore, bitubular breadth and bizygomatic breadth of the skulls were used to estimate body mass (Plavcan 2003). Results did not differ in their level of significance if these species were excluded from the analyses, and therefore they were included.

Seasonality

Malagasy Lemurs. In lemurs, we measure experienced seasonality by using temporal variation in the consumption of the diet component with the highest nutritional value. The dietary data were taken from Hemingway and Bynum (2005), with additional recent studies added (table A4). In total, dietary data were available for 26 populations of 19 lemur species. The coefficient of variation (CV) in consumption of dietary components over a year was measured from the monthly means of the following food items: insects, fruit/seeds, flowers, young leaves, and mature leaves. From this, we calculated the CV in the item with the highest nutritional value eaten for more than 10% of the average feeding time (insects > fruit/seeds > flowers > young leaves > mature leaves), henceforth referred to as

"CV in diet." Second, the total nutritional value per month was calculated as the sum of each item times its quality (8 for insects, 5 for fruits, seeds and flowers, 3 for young leaves, and 1 for mature leaves; Langer 2003), yielding a coefficient of variation of net energy intake. Since field metabolic rates are too insufficiently studied, we assumed that energy expenditure is equal throughout the year.

Ideally, we would use diet variability, brain mass, and body mass of the same population for each lemur species. However, diet composition has generally been studied in populations different from those for which specimens were available in museums and from which brain sizes were measured. Therefore, we compiled values of brain and body mass sampled within a 100-km radius of the population in which diet composition was studied. However, results from an overall average of brain and body mass data set ($N = 19$) did not differ in their level of significance from results from this reduced conservative data set ($N = 15$); therefore, all of our results presented here are based on the larger data set.

We tested whether experienced seasonality matches environmental seasonality reflected by plant productivity and climatic seasonality. Van Schaik and Pfannes (2005) showed that tropical primates living in climatically seasonal habitats experience seasonality in resource availability. In their study, three measures of precipitation variation correlate positively with flush/flower/fruit availability: first, the coefficient of variation (CV = SD/mean); second, the mean vector length (r) that estimates the concentration of precipitation over the year (Batschelet 1981); third, P2T as a measure of the length of the dry season, a dry month is defined when its total precipitation is less than two times the mean temperature (Walter 1971).[1] We calculated these three seasonality measures (CV, r, and P2T) from monthly precipitation means and standard deviation in temperature. In western Madagascar, water is estimated to be the major limiting factor for plant production, whereas in eastern Madagascar, irradiance is thought to limit plant productivity (Boisvenue and Running 2006). All these climatic seasonality measures were calculated from the WorldClim database (Hijmans et al. 2005) using ArcGIS 9.1. In addition, we extracted the normalized difference vegetation index (see Myneni et al. 2005), a more direct measure of plant productivity, from the GIMMS database (Tucker et al. 2005) and calculated its seasonality using the CV.

African Lorises. For lorises, diet composition data are not available in sufficient detail to study monthly variation (Charles-Dominique 1974; Harcourt 1986). Fortunately, however, African lorises are homogeneous in their diet and lifestyle, and we therefore assume that environmental seasonality is a good proxy of experienced seasonality in this group. We calculated the same climatic measures as described above (CV in precipitation, r in precipitation, P2T [the number of dry months], and SD in temperature). However, in contrast to the situation in Malagasy lemurs, plant productivity is probably not reflecting experienced seasonality in lorises, since in equatorial Africa plant productivity does not correlate with insect availability (Wolda 1978; Coley and Barone 1996).

[1] P2T = number of dry months per year, with a dry month defined by precipitation (P; mL) < 2 × temperature (T; degrees C). For example, a month with a mean temperature of 30°C and less than 60 mL of precipitation will be considered dry.

Analyses of Brain Size Variation

First, we tested whether seasonality was an energetic constraint on brain size by examining the relationship between relative brain size and seasonality. In the lemurs, results of analyses using the CV of only the highest nutritional-value food item were very similar to those obtained using CV of net energy intake (dietary items times their quality). Hence, we report only the first set of results.

Additionally we performed a within-genus comparison in the lemurs, using residual brain sizes of each species from a brain against body mass regression within lemurs (table A3 in the online edition of the *American Naturalist*). We compared the relative brain sizes from taxa inhabiting the western, more seasonal part of Madagascar with their sister taxa inhabiting the eastern, less seasonal part of Madagascar. We expected that the sister taxa living in the western part would have relatively smaller brains than the ones living in the eastern part.

Second, to test whether lemurs additionally cognitively buffer seasonality, we examined the relationship between relative brain size and the difference between the seasonality of the habitat (CV in precipitation and CV in NDVI) and the seasonality in net energy intake (CV in dietary items times their quality). Here, taking the complete net energy intake into account is critical since we were interested in how much buffering through feeding on fallback foods is taking place during the lean season.

We controlled for phylogenetic relatedness using phylogenetic generalized least squares (PGLS) analyses in R (R Development Core Team 2010) with the CAIC package (Orme et al. 2009). Strepsirrhine relations are debated (Mittermeier et al. 2008), and therefore, we ran all analyses with four different, recently suggested trees (Bininda-Emonds et al. 2007; Horvath et al. 2008; Orlando et al. 2008; Arnold et al. 2010). Results remained largely unaffected by the choice of phylogenetic tree (see table A1 in the online edition of the *American Naturalist*), and we therefore report only the results based on one of them

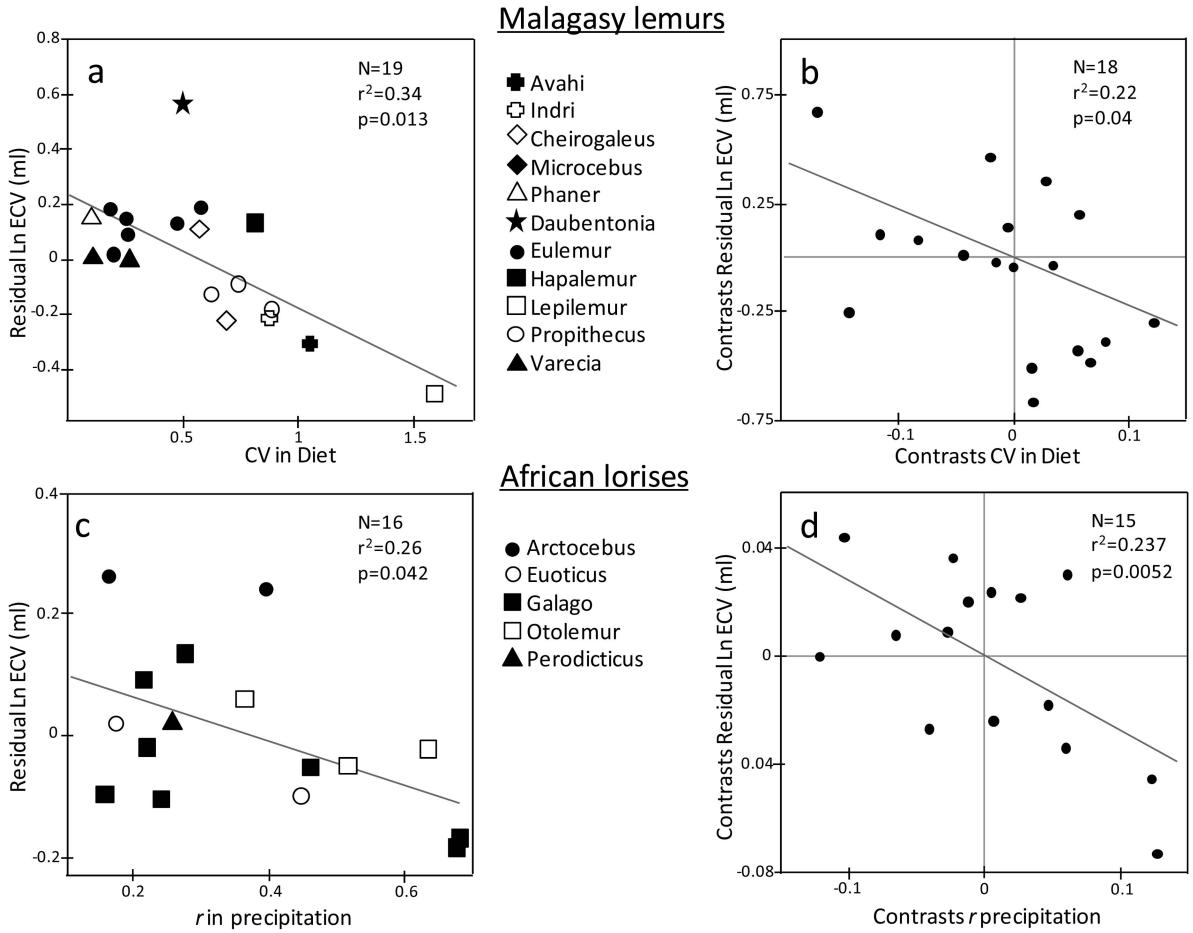

Figure 2: Correlation between brain size and experienced seasonality (CV in diet) of lemurs in the species values (*a*) and independent contrasts (*b*), and the correlation between brain size and precipitation seasonality (*r* in precipitation) of lorises in the species values (*c*) and in dependent contrasts (*d*). In both taxa, experienced seasonality shows a significant negative influence on brain size.

(fig. A1 in the online edition of the *American Naturalist*). The lemur tree is based on work by Horvath et al. (2008), with the following species added according to their location and distances in version 2 of the consensus tree based on the Bayesian primate phylogeny from the 10k Trees Project (Arnold et al. 2010): *Hapalemur alaotrensis*, *Hapalemur occidentalis*, *Propithecus deckenii*, *Propithecus verreauxi*, *Propithecus edwardsi*, *Avahi occidentalis*, *Avahi laniger*, *Indri indri*, *Lepilemur mustelinus*, *Lepilemur edwardsi*, *Lepilemur dorsalis*, *Lepilemur microdon*, *Cheirogaleus major*, and *Microcebus rufus*. Furthermore, *Phaner pallescens*, *Phaner furcifer*, and *Cheirogaleus ravus* were added according to relations reported by Groves (2000) and Pastorini et al. (2001). Results did not differ if the latter three species were removed from the analyses; therefore, they are included in the reported results. The loris phylogeny was based on version 2 of the consensus tree from the 10k Trees Project (Arnold et al. 2010), with *Galago thomasi*, *Galago matschiei*, *Otolemur monteiri*, and *Euoticus pallidus* added according to Bininda-Emonds et al. (2007). As the parameter λ was always close to 1, indicating a strong phylogenetic component in the data, we show independent contrast values in figure 2. Brain and body variables were log transformed before analysis, and statistical tests were parametric least squares regressions, using JMP 7.0.2.

In all multiple regressions, body mass was included as a covariate, and residuals of brain size versus body mass are shown in graphs. Diurnality, degree of folivory, and group size have been shown to correlate with brain size in primates (reviewed in Healy and Rowe 2007); hence, we took these possibly confounding variables into account. Torpor or hibernation is the most extreme adaptation to cope with seasonal energy shortages and is found within only two lemur genera, *Cheirogaleus* spp. and *Microcebus*

spp. (reviewed by Schülke and Ostner 2007). Although it is unknown how the metabolic requirements of brain tissue are affected by torpor or hibernation in primates, these two genera are among the least encephalized of all primates, and a possible relationship between periodic torpor and brain size can be expected. Therefore, we selected a model with the best fit according to the Information Theory Criterion (Akaike 1974), including the following possible covariables: body mass, variability in diet, hibernation/torpor, diurnality (nocturnal, diurnal, cathemeral), degree of folivory (yearly average percentage of leaves in the diet), and maximum group size.

Results

Experienced versus Environmental Seasonality

We tested the predictive power of monthly variation in plant productivity and climate for experienced seasonality in the Malagasy lemurs. Only the CV in plant productivity (NDVI) and the concentration (*r*) in precipitation were significantly correlated with CV in diet (NDVI: $r^2 = 0.31$, $P = .014$; *r* in precipitation: $r^2 = 0.23$, $P = .037$), whereas the other measures of climatic seasonality showed only a trend or no significance (CV in precipitation: $r^2 = 0.20$, $P = .05$; P2T (number of dry months): $r^2 = 0.13$, $P = .13$; SD in temperature: $r^2 = 0.03$, $P = .48$). The low coefficient of determination r^2 indicated that variation in plant productivity (CV in NDVI) and precipitation (*r* in precipitation) were rather weak predictors for experienced seasonality in the lemurs.

Seasonality as an Energetic Constraint on Brain Size

In lemurs, variation in diet was significantly negatively correlated with brain size (PGLS: $t = -3.35$, $P = .004$, $\lambda = 0.999$; fig. 2*a*, 2*b*), indicating that lemur species with more variation in the consumption of their preferred food item have smaller brains. The best-fit model according to Akaike's Information Theory Criterion included body mass, CV in diet, and group size, with a significant influence of body mass and CV in diet (table 1). The relationships between brain size and variation in precipitation and plant productivity were all negative for the lemurs, but only CV in plant productivity and length of dry season (P2T) showed a significant correlation (table 1).

With our within-genus comparison in the lemurs, we confirmed that taxa inhabiting the western, more seasonal part of Madagascar evolved relatively smaller brains than their sister taxa living on the eastern side (table A2 in the online edition of the *American Naturalist*). The effect is stronger within the smaller sister taxa (*Microcebus*, *Cheirogaleus*) than the larger ones (*Propithecus*).

Table 1: Phylogenetic generalized least squares best-fit models between relative brain size (corrected for body mass) and climatic seasonality in Malagasy lemurs and African lorises

	Malagasy lemurs (climate: $N = 36$; diet: $N = 19$)			African lorises ($N = 16$)		
Seasonality measure	*t* ratio	*P*	λ	*t* ratio	*P*	λ
CV in diet	−3.35	**.004**	1.00			
CV in plant productivity	−2.92	**.007**	.97	−.32	.757	.72
r in precipitation	−.94	.355	.95	−2.94	**.011**	.98
CV in precipitation	−.91	.368	.95	−2.19	**.047**	1.00
P2T	2.39	**.023**	.99	2.03	.062	1.00
SD in temperature	−.84	.406	.93	−2.65	**.020**	1.00

Note: For the lemurs, dietary type and hibernation are included in the best-fit model for the climatic seasonality measures. In the best-fit models for experienced seasonality (CV in diet), hibernation is included as a covariable (results remain the same if hibernation is excluded; see table A3 in the online edition of the *American Naturalist*). Since the African lorises do not differ in dietary type or nocturnality and group size did not have an effect, the model included only brain size, body mass, and climatic seasonality. Significant *P* values are shown in boldface. All λ values are not significantly different from 0.

In the African lorises, we found a significant negative correlation between relative brain size and all environmental variables except length of dry season (P2T), where we found a strong trend (table 1; fig. 2*c*, 2*d*). As expected, plant productivity and relative brain size were not correlated in this group.

Seasonality as a Cognitive Challenge

The negative correlations we found between relative brain size and experienced seasonality support the expensive brain framework. However, cognitive buffer effects, predicted by the cognitive buffer hypothesis, could still apply in addition to the energetic constraints since within lemurs, experienced seasonality, as proxied by temporal variation in energy intake, is not well predicted by environmental seasonality (see above). Therefore, we tested whether a combination of energetic constraints and cognitive buffer effects applied here. We found a positive trend between relative brain size and the difference between experienced seasonality and environmental seasonality (experienced seasonality minus seasonality in plant productivity: $N = 19$, species level: $t = 2.13$, $P = .05$, PGLS: $P = .14$, $\lambda = 1.00$; experienced seasonality minus seasonality in precipitation: $N = 19$, species level: $t = 1.83$, $P = .09$, PGLS: $P = .11$, $\lambda = 1.00$). We found no difference in the results when we controlled for possible confounding variables (hibernation/torpor, diurnality, degree of folivory, and maximum group size).

Discussion

In both Malagasy lemurs and African lorises, we found that species experiencing pronounced seasonal changes in food availability have relatively smaller brains, controlling for possibly confounding variables such as body mass, phylogenetic relatedness, diet, and specialized adaptations. For the lemurs, experienced seasonality as proxied by variation in intake of preferred food was more strongly correlated with brain size than were either plant productivity or climatic seasonality, indicating the occurrence of buffer effects. In the African lorises, on the other hand, we assume that climatic seasonality aptly reflects the conditions experienced by the animals due to the dietary and behavioral homogeneity of this group. Although we were not able to test this assumption due to the lack of detailed data on diet in this group, the negative relationship we found between relative brain size and climatic seasonality lends support to our expectation. In contrast to lemurs, plant productivity is not relevant in lorises, as availability of their most important diet component, insects, is influenced more by rainfall than by leaf production (Wolda 1978; Coley and Barone 1996). This discrepancy between rainfall and leaf production can arise when plant productivity is limited by irradiance, not rainfall, as is the case in central Africa (Wright and van Schaik 1994). Thus, the observed negative correlation between rainfall seasonality and brain size in African lorises supports our predictions.

Our results therefore unequivocally support the energetic view of brain size evolution proposed by Aiello and Wheeler (1995) and Martin (1996) among others. Recently, Isler and van Schaik (2006*b*; 2009) emphasized the utility of a broad theoretical framework to examine the energetic aspects of brain size evolution, which allows specific predictions to be tested. Many of these have already been confirmed (Isler and van Schaik 2006*a*, 2006*b*, 2009). Accordingly, several authors now stress the importance of considering energetic constraints (e.g., Dunbar 2009), which have nonetheless rarely been considered in predictions or tests of cognitive buffer effects. In this study we show that ecological conditions are correlated with encephalization in strepsirrhine primates. As predicted, recurring periods of food scarcity evolutionarily constrain brain size because net energy availability is reduced during these times. In more seasonal habitats, primates evolved strategies that allow them to expend less energy to compensate for the reduction in energy intake, such as reproducing seasonally (assuming the reproductive cycle can be completed in less than a year), switching to energetically less valuable but widely available fallback foods, or even entering torpor or hibernation during the lean periods. Nevertheless, our results show that such physiological buffers do not sufficiently compensate for reduced energy availability to provide equal opportunities for enlarged brain size as compared to species living in less variable habitats. Moreover, our within-genus comparison within the lemurs provides evidence that these constraints can work in a relatively short time (1–7 million years).

The negative correlation between brain size and habitat seasonality would be even stronger if larger brains did not also have some benefit. A cognitive buffer would allow species to dampen the fluctuations in the supply of preferred foods and thus limit fluctuations in their energy intake to a lower level than expected by finding or accessing hidden or protected food sources (e.g., extractive foraging) or by switching to other microhabitats. In this case, seasonality of the habitat might act as a positive selection pressure for a relatively large brain that would counteract the effect of energy constraints. One might therefore expect a positive correlation between brain size and the difference between habitat seasonality and experienced seasonality, that is, temporal variation in dietary energy content (fig. 1*b*). The weakness of the correlation found in this study may be explained by various shortcomings of the data set. In combination with a relatively small sample, the studies of diet composition may be too heterogeneous, depending on observation protocols and characteristics of the study sites. The resulting error could weaken the correlations if phylogenetic methods are used (Martin et al. 2005). On the other hand, the weak result could simply reflect the fact that a cognitive buffer effect is rare within lemurs, as almost all species experience a high degree of perceived habitat seasonality. The only obvious exception is the aye-aye (*Daubentonia madagascariensis*), the single extant member of a family that split off from the rest of the lemurs at least 60 million years ago (phylogenetic relations are debated; see Martin 2000). This peculiar primate's brain is exceptionally large, within the range of anthropoid primates, and is matched by a relatively high basal metabolic rate for a lemur (Isler et al. 2008; Barrickman and Lin 2010). Aligning these two characteristics, the experienced seasonality of the aye-aye seems to be low; as an extractive forager its diet consists of high-quality food sources throughout the year (Sterling 1994), and it is the only lemur that does not have a breeding season (Beattie et al. 1992; Sterling 1994). Thus, extractive foraging is apparently acting as a cognitive buffer in the aye-aye.

It would be interesting to expand our study to the extinct lemurs that were mostly larger in body mass and may have shown extreme life-history characteristics exceeding the range of extant species (Catlett et al. 2010). The presumably most folivorous taxon, *Megaladapis*, has the relatively smallest brain, and the giant lemur thought to have a diet similar to that of the aye-aye, *Archaeolemur*, has the relatively largest brain (Godfrey et al. 2004; Schwartz et

al. 2005). Assessing the degree of experienced seasonality is difficult for extinct species, but current reconstructions of diet and lifestyle for those species with known brain size are in accordance with our findings. The two species with the relatively largest brains (*Archaeolemur* and *Hadropithecus*) are those for which the assumption of a nonseasonal breeding pattern seems most appropriate (Catlett et al. 2010). Interestingly, these authors found that (large) brain size is a better predictor of (low) reproductive rates than is body mass, independently confirming a more general trend found in eutherian mammals (Isler and van Schaik 2009). More detailed studies on the relationships between ecological adaptations, life-history traits, and brain size are warranted in the extinct lemur species.

The groups analyzed in this study were small to medium-sized primates that were relatively small brained compared to anthropoid primates but still relatively large brained compared to other mammals of similar body size. Therefore, both Malagasy lemurs and African lorises use a relatively large percentage of their basal metabolism to maintain their brains and can therefore be expected to experience stronger energetic constraints on brain size than, for instance, cercopithecoid monkeys. The within-genus comparison among the lemurs also showed a stronger effect within the smaller sister taxa (*Microcebus*, *Cheirogaleus*) than in the larger ones (*Propithecus*). It remains to be seen whether the negative correlation between perceived seasonality and brain size also exists in large-bodied primates or whether cognitive buffer effects will be stronger.

In conclusion, this study of strepsirrhine primates supports the argument that seasonality has acted primarily as a constraint rather than a positive selective pressure on brain size. We propose that the effect of seasonality on strepsirrhine brain sizes and the reduced brain size of island dwarfs are special cases of a far more general phenomenon. In general, conditions under which animals are forced to deal with periods of unavoidable food shortage, a result of seasonality (this study), living on islands (Köhler and Moyà-Solà 2004; Weston and Lister 2009), and El Niño droughts (Taylor and van Schaik 2007), should lead to relatively smaller brains.

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Literature Cited

Aiello, L. C., and P. Wheeler. 1995. The expensive-tissue hypothesis: the brain and the digestive-system in human and primate evolution. Current Anthropology 36:199–221.

Akaike, H. 1974. A new look at statistical-model identification. IEEE Transactions on Automatic Control 19:716–723.

Albrecht, G. H., P. D. Jenkins, and L. R. Godfrey. 1990. Ecogeographic size variation among the living and subfossil prosimians of Madagascar. American Journal of Primatology 22:1–50.

Allmann, J., T. McLaughlin, and A. Hakeem. 1993. Brain-weight and life-span in primate species. Proceedings of the National Academy of Sciences of the USA 90:118–122.

Arnold, C., L. J. Matthews, and C. L. Nunn. 2010. The 10k Trees website: a new online resource for primate phylogeny. Evolutionary Anthropology 19:114–118.

Barrickman, N. L., and M. J. Lin. 2010. Encephalization, expensive tissues, and energetics: an examination of the relative costs of brain size in strepsirrhines. American Journal of Physical Anthropology. doi:10.1002/ajpa.21354.

Batschelet, E. 1981. Circular statistics in biology. Academic Press, London.

Beattie, J. C., A. T. C. Feistner, N. M. O. Adams, P. Barker, and J. B. Carroll. 1992. First captive breeding of the aye-aye, *Daubentonia madagascariensis*. Dodo 28:23–30.

Bininda-Emonds, O. R. P., M. Cardillo, K. E. Jones, R. D. E. MacPhee, R. M. D. Beck, R. Grenyer, S. A. Price, et al. 2007. The delayed rise of present-day mammals. Nature 446:507–512.

Boisvenue, C., and S. W. Running. 2006. Impacts of climate change on natural forest productivity: evidence since the middle of the 20th century. Global Change Biology 12:862–882.

Catlett, K. K., G. T. Schwartz, L. R. Godfrey, and W. L. Jungers. 2010. "Life history space": a multivariate analysis of life history variation in extant and extinct Malagasy lemurs. American Journal of Physical Anthropology 143:391–404.

Charles-Dominique, P. 1974. Ecology and feeding behavior of five sympatric lorisids in Gabon. Pages 131–150 *in* R. D. Martin, G. A. Doyle, and A. C. Walker, eds. Prosimian biology. Duckworth, London.

Coley, P. D., and J. A. Barone. 1996. Herbivory and plant defenses in tropical forests. Annual Review of Ecology and Systematics 27: 305–335.

Dausmann, K. H., J. Glos, J. U. Ganzhorn, and G. Heldmaier. 2004. Physiology: hibernation in a tropical primate: even in the wound-down hibernating state, this lemur can warm up without waking up. Nature 429:825–826.

Dewar, R. E., and A. F. Richard. 2007. Evolution in the hypervariable environment of Madagascar. Proceedings of the National Academy of Sciences of the USA 104:13723–13727.

Dunbar, R. I. M. 2009. The social brain hypothesis and its implications for social evolution. Annals of Human Biology 36:562–572.

Eeley, H. A. C., and R. A. Foley. 1999. Species richness, species range size and ecological specialisation among African primates: geographical patterns and conservation implications. Biodiversity and Conservation 8:1033–1056.

Filin, I., and Y. Ziv. 2004. New theory of insular evolution: unifying the loss of dispersability and body-mass change. Evolutionary Ecology Research 6:115–124.

Fish, J. L., and C. A. Lockwood. 2003. Dietary constraints on encephalization in primates. American Journal of Physical Anthropology 120:171–181.

Ganzhorn, J. U. 1995. Cyclones over Madagascar: fate or fortune. Ambio 24:124–125.

Ganzhorn, J. U., J. Fietz, E. Rakotovao, D. Schwab, and D. Zinner. 1999. Lemurs and the regeneration of dry deciduous forest in Madagascar. Conservation Biology 13:794–804.

Genoud, M. 2002. Comparative studies of basal rate of metabolism in primates. Evolutionary Anthropology 11(suppl. 1):108–111.

Godfrey, L. R., K. E. Samonds, W. L. Jungers, and M. R. Sutherland. 2001. Teeth, brains, and primate life histories. American Journal of Physical Anthropology 114:192–214.

Godfrey, L. R., G. M. Semprebon, W. L. Jungers, M. R. Sutherland, E. L. Simons, and N. Solounias. 2004. Dental use wear in extinct lemurs: evidence of diet and niche differentiation. Journal of Human Evolution 47:145–169.

Groves, C. P. 2000. The genus *Cheirogaleus*: unrecognized biodiversity in dwarf lemurs. International Journal of Primatology 21:943–962.

Harcourt, C. 1986. Seasonal variation in the diet of South African galagos. International Journal of Primatology 7:491–506.

Healy, S. D., and C. Rowe. 2007. A critique of comparative studies of brain size. Proceedings of the Royal Society B: Biological Sciences 274:453–464.

Hemingway, C. A., and N. Bynum. 2005. The influence of seasonality on primate diet and ranging. Pages 57–104 *in* D. A. Brockman and C. P. van Schaik, eds. Seasonality in primates. Cambridge University Press, New York.

Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25:1965–1978.

Horvath, J. E., D. W. Weisrock, S. L. Embry, I. Fiorentino, J. P. Balhoff, P. Kappeler, G. A. Wray, et al. 2008. Development and application of a phylogenomic toolkit: resolving the evolutionary history of Madagascar's lemurs. Genome Research 18:489–499.

Isler, K., and C. P. van Schaik. 2006*a*. Costs of encephalization: the energy trade-off hypothesis tested on birds. Journal of Human Evolution 51:228–243.

———. 2006*b*. Metabolic costs of brain size evolution. Biology Letters 2:557–560.

———. 2009. The expensive brain: a framework for explaining evolutionary changes in brain size. Journal of Human Evolution 57: 392–400.

Isler, K., E. C. Kirk, J. M. A. Miller, G. A. Albrecht, B. R. Gelvin, and R. D. Martin. 2008. Endocranial volumes of primate species: scaling analyses using a comprehensive and reliable data set. Journal of Human Evolution 55:967–978.

Janson, C. H., and C. A. Chapman. 1999. Resources and primate community structure. Pages 237–267 *in* J. G. Fleagle, C. H. Janson, and K. E. Reed, eds. Primate communities. Cambridge University Press, Cambridge.

Janson, C. H., and J. Verdolin. 2005. Seasonality of primate births in relation to climate. Pages 307–350 *in* D. A. Brockman and C. P. van Schaik, eds. Seasonality in primates. Cambridge University Press, New York.

Kappeler, P. M. 1997. Determinants of primate social organization: comparative evidence and new insights from Malagasy lemurs. Biological Reviews of the Cambridge Philosophical Society 72:111–151.

Köhler, M., and S. Moyà-Solà. 2004. Reduction of brain and sense organs in the fossil insular bovid *Myotragus*. Brain Behavior and Evolution 63:125–140.

Krilowicz, B. L., S. F. Glotzbach, and H. C. Heller. 1988. Neuronal activity during sleep and complete bouts of hibernation. American Journal of Physiology 255:R1008–R1019.

Langer, P. 2003. Lactation, weaning period, food quality, and digestive tract differentiations in eutheria. Evolution 57:1196–1215.

Lehman, S. M., M. Mayor, and P. C. Wright. 2005. Ecogeographic size variations in sifakas: a test of the resource seasonality and resource quality hypotheses. American Journal of Physical Anthropology 126:318–328.

Lomolino, M. V. 2005. Body size evolution in insular vertebrates: generality of the island rule. Journal of Biogeography 32:1683–1699.

Lukas, W. D., and B. C. Campbell. 2000. Evolutionary and ecological aspects of early brain malnutrition in humans. Human Nature 11: 1–26.

MacLean, E. L., N. L. Barrickman, E. M. Johnson, and C. E. Wall. 2009. Sociality, ecology, and relative brain size in lemurs. Journal of Human Evolution 56:471–478.

Martin, R. D. 2000. Origins, diversity and relationships of lemurs. International Journal of Primatology 21:1021–1049.

———. 1996. Scaling of the mammalian brain: the maternal energy hypothesis. News in Physiological Sciences 11:149–156.

Martin, R. D., M. Genoud, and C. K. Hemelrijk. 2005. Problems of allometric scaling analysis: examples from mammalian reproductive biology. Journal of Experimental Biology 208:1731–1747.

Mink, J. W., R. J. Blumenschine, and D. B. Adams. 1981. Ratio of central nervous system to body metabolism in vertebrates: its constancy and functional basis. American Journal of Physiology 241: R203–R212.

Mittermeier, R., J. Ganzhorn, W. Konstant, K. Glander, I. Tattersall, C. Groves, A. Rylands, et al. 2008. Lemur diversity in Madagascar. International Journal of Primatology 29:1607–1656.

Myneni, R., W. T. B. Yang, N. Shabanov, and Y. Knyazikhin. 2005. Global products of vegetation leaf area and fraction absorbed PAR from MODIS sensors onboard NASA *Terra* and *Aqua* satellites. Pages 200–202 *in* S. Liang, J. Liu, X. Li, R. Liu, and M. Schaepman, eds. Proceedings of the 9th International Symposium on Physical Measurements and Signatures in Remote Sensing. Beijing, October 17–19.

Niven, J. E. 2007. Brains, islands and evolution: breaking all the rules. Trends in Ecology & Evolution 22:57–59.

Nunn, C. L. 1999. The number of males in primate social groups: a comparative test of the socioecological model. Behavioral Ecology and Sociobiology 46:1–13.

Orlando, L., S. Calvignac, C. Schnebelen, C. J. Douady, L. R. Godfrey,

and C. Hanni. 2008. DNA from extinct giant lemurs links archaeolemurids to extant indriids. BMC Evolutionary Biology 8: 121–130.

Orme, D., R. P. Freckleton, G. Thomas, T. Petzoldt, and S. Fritz. 2009. CAIC: comparative analyses using independent contrasts. R package version 1.0.4-94/r94, http://r-forge.r-project.org/projects/caic.

Ostner, J., P. M. Kappeler, and M. Heistermann. 2002. Seasonal variation and social correlates of androgen excretion in male red-fronted lemurs (*Eulemur fulvus rufus*). Behavioral Ecology and Sociobiology 52:485–495.

Pastorini, J., R. D. Martin, P. Ehresmann, E. Zimmermann, and M. R. J. Forstner. 2001. Molecular phylogeny of the lemur family Cheirogaleidae (primates) based on mitochondrial DNA sequences. Molecular Phylogenetics and Evolution 19:45–56.

Pettorelli, N., J. O. Vik, A. Mysterud, J. M. Gaillard, C. J. Tucker, and N. C. Stenseth. 2005. Using the satellite-derived NDVI to assess ecological responses to environmental change. Trends in Ecology & Evolution 20:503–510.

Plavcan, J. M. 2003. Scaling relationships between craniofacial sexual dimorphism and body mass dimorphism in primates: implications for the fossil record. American Journal of Physical Anthropology 120:38–60.

Plavcan, J. M., C. P. van Schaik, and W. S. McGraw. 2005. Seasonality, social organization, and sexual dimorphism in primates. Pages 401–442 *in* D. A. Brockman and C. P. van Schaik, eds. Seasonality in primates. Cambridge University Press, New York.

R Development Core Team. 2010. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Rowe, N. 1996. The pictorial guide to the living primates. Pogonias, New York.

Schuck-Paim, C., W. J. Alonso, and E. B. Ottoni. 2008. Cognition in an ever-changing world: climatic variability is associated with brain size in Neotropical parrots. Brain Behavior and Evolution 71:200–215.

Schülke, O., and J. Ostner. 2007. Physiological ecology of cheirogaleid primates: variation in hibernation and torpor. Acta Ethologica 10: 13–21.

Schwartz, G., P. Mahoney, L. Godfrey, and W. Jungers. 2005. Dental development and life history in one of the largest subfossil Malagasy lemurs, *Megaladapis edwardsi*. Journal of Vertebrate Paleontology 25:111a–112a.

Shultz, S., and R. I. M. Dunbar. 2007. The evolution of the social brain: anthropoid primates contrast with other vertebrates. Proceedings of the Royal Society B: Biological Sciences 274:2429–2436.

Smith, R. J., and W. L. Jungers. 1997. Body mass in comparative primatology. Journal of Human Evolution 32:523–559.

Sol, D., L. Lefebvre, and J. D. Rodriguez-Teijeiro. 2005. Brain size, innovative propensity and migratory behaviour in temperate Palaearctic birds. Proceedings of the Royal Society B: Biological Sciences 272:1433–1441.

Sterling, E. J. 1994. Evidence for nonseasonal reproduction in wild aye-ayes (*Daubentonia madagascariensis*). Folia Primatologica 62: 46–53.

Strier, K. B., T. E. Ziegler, and D. J. Wittwer. 1999. Seasonal and social correlates of fecal testosterone and cortisol levels in wild male muriquis (*Brachyteles arachnoides*). Hormones and Behavior 35:125–134.

Taylor, A. B., and C. P. van Schaik. 2007. Variation in brain size and ecology in *Pongo*. Journal of Human Evolution 52:59–71.

Tucker, C. J., J. E. Pinzon, M. E. Brown, D. A. Slayback, E. W. Pak, R. Mahoney, E. F. Vermote, et al. 2005. An extended AVHRR 8-km NDVI dataset compatible with MODIS and SPOT vegetation NDVI data. International Journal of Remote Sensing 26:4485–4498.

van Schaik, C. P., and K. R. Pfannes. 2005. Tropical climates and phenology: a primate perspective. Pages 23–54 *in* D. A. Brockman and C. P. van Schaik, eds. Seasonality in primates. Cambridge University Press, New York.

Walter, H. 1971. Ecology of tropical and subtropical vegetation. Oliver & Boyd, Edinburgh.

Weston, E. M., and A. M. Lister. 2009. Insular dwarfism in hippos and a model for brain size reduction in *Homo floresiensis*. Nature 459:85–88.

Winkler, H., B. Leisler, and G. Bernroider. 2004. Ecological constraints on the evolution of avian brains. Journal of Ornithology 145:238–244.

Wolda, H. 1978. Fluctuations in abundance of tropical insects. American Naturalist 112:1017–1045.

Wright, P. C. 1999. Lemur traits and Madagascar ecology: coping with an island environment. Yearbook of Physical Anthropology 42:31–72.

Wright, S. J., and C. P. van Schaik. 1994. Light and the phenology of tropical trees. American Naturalist 143:192–199.

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